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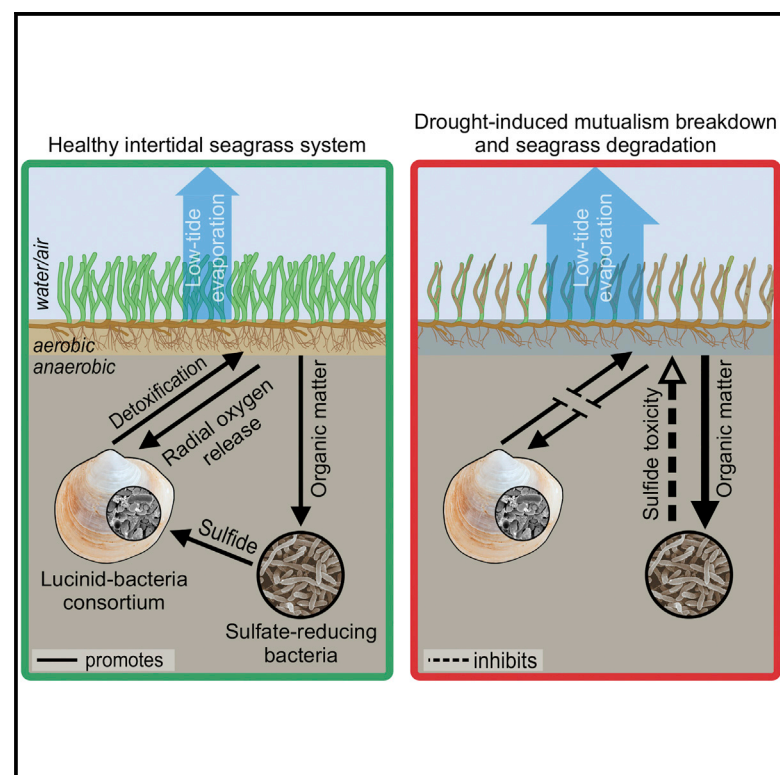
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Current Biology

Drought, Mutualism Breakdown, and Landscape-Scale Degradation of Seagrass Beds

Graphical Abstract



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In Brief

Concerns grow that disruption of mutualisms may amplify marine ecosystem degradation. De Fouw et al. show how drought triggered the breakdown of a facultative mutualism that accelerated landscape-scale intertidal seagrass collapse, revealing a hidden risk of mutualism dependency in marine ecosystems beyond the well-known obligate coral symbiosis.

Highlights

- Climate extremes may cause breakdown of the facultative seagrass-lucinid mutualism
- Loss of this mutualistic feedback can amplify seagrass ecosystem degradation
- Risk of marine mutualism breakdown goes beyond the obligate coral symbiosis
- These mechanisms need inclusion in marine conservation and restoration approaches



Drought, Mutualism Breakdown, and Landscape-Scale Degradation of Seagrass Beds

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SUMMARY

In many marine ecosystems, biodiversity critically depends on foundation species such as corals and seagrasses that engage in mutualistic interactions [1–3]. Concerns grow that environmental disruption of marine mutualisms exacerbates ecosystem degradation, with breakdown of the obligate coral mutualism (“coral bleaching”) being an iconic example [2, 4, 5]. However, as these mutualisms are mostly facultative rather than obligate, it remains unclear whether mutualism breakdown is a common risk in marine ecosystems, and thus a potential accelerator of ecosystem degradation. Here, we provide evidence that drought triggered landscape-scale seagrass degradation and show the consequent failure of a facultative mutualistic feedback between seagrass and sulfide-consuming lucinid bivalves that in turn appeared to exacerbate the observed collapse. Local climate and remote sensing analyses revealed seagrass collapse after a summer with intense low-tide drought stress. Potential analysis—a novel approach to detect feedback-mediated state shifts—revealed two attractors (healthy and degraded states) during the collapse, suggesting that the drought disrupted internal feedbacks to cause abrupt, patch-wise degradation. Field measurements comparing degraded patches that were healthy before the collapse with patches that remained healthy demonstrated that bivalves declined dramatically in degrading patches with associated high sediment sulfide concentrations, confirming the breakdown of the mutualistic seagrass-lucinid

feedback. Our findings indicate that drought triggered mutualism breakdown, resulting in toxic sulfide concentrations that aggravated seagrass degradation. We conclude that external disturbances can cause sudden breakdown of facultative marine mutualistic feedbacks. As this may amplify ecosystem degradation, we suggest including mutualisms in marine conservation and restoration approaches.

RESULTS

Mutualisms are important drivers of global biodiversity and ecosystem functioning, as many organisms are directly involved in networks of beneficial interactions [4, 6, 7]. A vast majority of terrestrial plants depends on mutualistic partnerships [6, 7], and in marine ecosystems, ecosystem-structuring foundation species such as corals, kelp, salt marsh plants, mangroves, and seagrasses may depend on them to decrease physical stress or gain resources [1–3]. Mounting evidence suggests that global change can disrupt such mutualistic feedback loops [2, 4, 8, 9], potentially accelerating habitat degradation [1, 2, 4]. Coral-bleaching events (i.e., expulsion of endosymbiotic algae) are an iconic example of environmental changes (e.g., global warming) leading to the breakdown of an obligate mutualism and ecosystem degradation [2, 5]. Similar to coral reefs, many other marine ecosystems shaped by mutualism-dependent foundation species also exhibit sudden and large-scale declines [10, 11]. However, in contrast to the obligate coral symbiosis, the mutualisms in these ecosystems are facultative [1] and can vary in strength depending on prevailing conditions [3]. Therefore, it remains unclear whether mutualism breakdown due to environmental change is a general risk inherent to mutualism-dependent marine ecosystems.

Here we investigate the hypotheses that (1) similar to the obligate coral symbiosis, climatic extremes can trigger sudden breakdown of a facultative mutualism between seagrass and

sulfide-consuming lucinid bivalves, and (2) the loss of this self-sustaining mutualistic feedback has the potential to exacerbate seagrass ecosystem degradation. Seagrass beds are essential for coastal zones worldwide because they provide coastal protection, act as carbon and nutrient sinks, and serve as vital habitat for many species [12–14]. Seagrass ecosystems are currently degrading at an accelerating rate worldwide [13], and losses are often typified by sudden die-off. Such rapid declines have been attributed to climatic extremes such as storms, high seawater temperatures, and low-tide desiccation events in intertidal beds [12, 15–18], but also to the disruption of internal feedback mechanisms by environmental changes [11, 19]. Seagrass meadows increase water clarity by trapping suspended particles and stabilizing sediments, thereby facilitating their own growth [3, 11, 14]. This positive feedback, however, also results in a negative feedback as organic matter accumulates in the sediment, and its anaerobic decomposition involving sulfate-reducing bacteria yields toxic sulfide [3, 20, 21]. To prevent sulfide accumulation, seagrasses can engage a (recently discovered) mutualistic feedback loop with lucinid bivalves and their gill-inhabiting, sulfide-oxidizing bacteria [3, 12]. In return, the bivalves and their endosymbionts profit not only from sulfide that is indirectly provided by the seagrasses, but also from oxygen released by seagrass roots [3, 22, 23].

To investigate our hypotheses, we studied a landscape-scale die-off event in the intertidal seagrass beds of Banc d'Arguin—a pristine Marine Protected Area in Mauritania (West Africa). In this tropical Sahara Desert climate, low-tide desiccation is a common stressor for seagrasses [24], but in 2010 and 2011 the region experienced exceptional drought and heat (with anomalies of +2°C to +3.5°C compared to long-term mean monthly temperatures) [25–27]. Using local climate data and remote sensing analyses of spatiotemporal seagrass dynamics, we investigated whether (1) the die-off could be related to low-tide desiccation stress caused by heat, wind, and/or drought extremes and (2) disruption of a feedback was an important accelerant of the observed decline. Finally, we carried out field measurements to examine the potential link between desiccation, seagrass die-off, and breakage of the mutualistic feedback.

Local Climate Analyses

Analyses of data from the nearest weather station suggest that in our study area, the summer of 2011 was exceptionally warm, windy, and dry, leading to a high evaporative demand (Supplemental Experimental Procedures). The number of extreme days in the warmest three months (August–October)—defined as days over the 95% percentile—was higher for all four variables included in our analyses (Figure 1). The number of recorded extremely hot and windy days in the warmest months was at least 1.3 times higher in 2011 compared to other years. More importantly, however, the number of extremes in the two most direct proxies of evaporation, and thus low-tide desiccation stress—dew point depression and water vapor pressure deficit [28]—was over five times higher in 2011.

Remote Sensing and Potential Analyses

To investigate spatiotemporal seagrass cover changes, we calculated the normalized difference vegetation index (NDVI) from Landsat imagery taken in 2007, 2009, 2011, and 2013

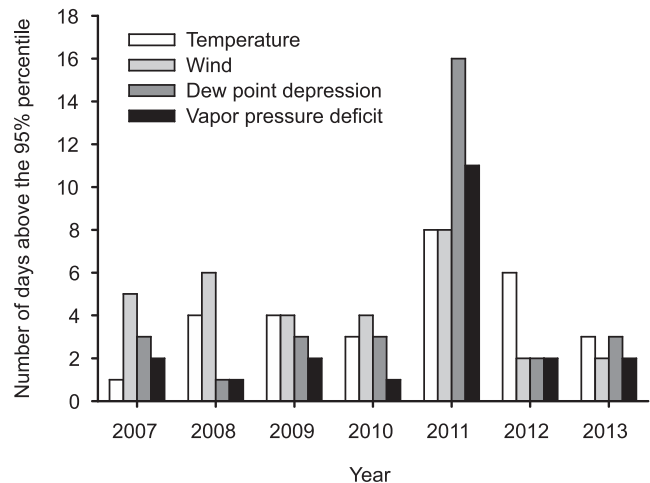


Figure 1. Number of Extreme Days in August to October Expressed as Days over the 95% Percentile in That Period

The number of days with extreme daily average temperature, wind speed, dew point depression, and water vapor pressure deficit in these three warmest months was higher in 2011 compared to other years. Differences are most pronounced for the two most direct measures of evaporation (and thus low-tide desiccation): dew point depression and water vapor pressure deficit.

and combined these analyses with ground observations (Supplemental Experimental Procedures; Figure S1). NDVI data indicate that degradation of the intertidal seagrass beds was initiated in 2011. After a small increase between 2007 and 2009, NDVI started to decrease, after which a system-wide 44% decline occurred in 2011–2013 (Figures 2A–2E). This landscape-scale NDVI decrease was supported by ground observations that showed a 50% decrease in seagrass cover between 2009 and 2013 (Figure 2F).

Next, we used potential analyses to test whether disruption of internal feedbacks by, for instance, the drought contributed to the sudden seagrass collapse. This analysis fits a probability density function to a state variable per interval along an environmental stress gradient. Potential analysis is based on the fact that if distinct ecosystem states exist due to the presence of strong internal feedbacks, transitions between these feedback-stabilized states or “attractors” will occur rapidly because intermediate states are inherently unstable [29]. As a consequence, multimodality in a fitted probability density function (i.e., multiple peaks in occurrence) indicates multiple attractors: maxima in occurrence are identified as attractors, and minima as transition thresholds (or “repellers”) between attractors (Supplemental Experimental Procedures) [30–32]. For our analysis, we estimated a probability density function from NDVI data per 0.1-m interval along the drought stress gradient approximated by elevation (i.e., exposure time).

In line with climate and NDVI analyses, potential analysis shows that seagrass degradation was most likely initiated by desiccation in 2011. The analysis also identified two distinct ecosystem states of high and low NDVI, indicating that the collapse was not simply the result of external environmental forcing, but that shifts between the two states were mediated by internal feedbacks (Figure 3). For 2007 and 2009, the analysis

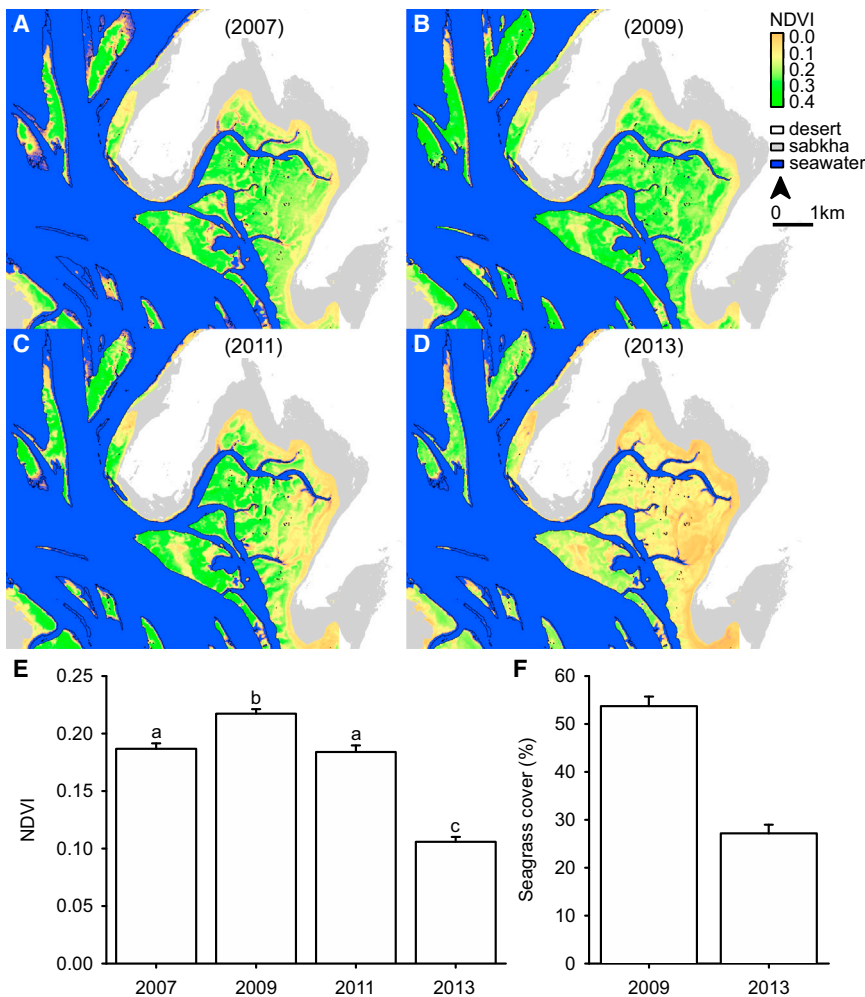


Figure 2. NDVI from 2007 to 2013 as Calculated from Landsat Imagery and Corresponding Ground Observations

(A–E) NDVI remained relatively stable from 2007 to 2011, after which a sharp 44% decrease followed between 2011 and 2013 ($F_{3,946} = 131.15$, $p < 0.001$; letters indicate post hoc groups). (F) Ground observations showed a 50% decrease between 2009 and 2013 ($F_{1,429} = 124.94$, $p < 0.001$). Error bars depict SEs ($n = 239$ and $n = 213$, respectively). See also Figure S1 and Table S1.

adjacent healthy patches at eight sites (four replicates per site) throughout our study area (Supplemental Experimental Procedures; Figure S1). Height measurements demonstrated that degraded patches were on average situated 6.7 cm higher than healthy areas (Figure 4A). Moreover, at low tide, we found that degraded patches were typically dry, with only 6% of the patches covered with a thin water film. In contrast, water drainage from higher toward lower patches resulted in the presence of a thin water film on the sediment surface at 88% of the healthy areas (Figure 4B). Apart from height and water, we detected no significant differences in general characteristics as indicated by sediment organic matter content ($11.9\% \pm 0.4\%$; mean \pm SE) and median grain size ($70.0 \pm 1.5 \mu\text{m}$).

Detailed investigations of the benthic community revealed that, since the onset

of degradation and our survey in 2012, aboveground seagrass biomass in degraded patches had been reduced by 89% (healthy: 124.3 ± 21.0 g dry weight per m^2 ; degraded: 13.9 ± 6.9 g). Densities of the small (~ 1 cm) dominant lucinid bivalve *Loripes lucinalis* were nine times lower in degraded patches (Figure 4C), while sulfide concentrations in the sediment pore water were over four times higher and showed an increase with depth (Figure 4D). Finally, a comparison of patches sampled both before (2009) and after the collapse (2013) confirmed that lucinids declined dramatically (four to five times) in degrading patches while remaining stable in healthy patches (Figure S3).

Field Measurements

The intertidal at Banc d'Arguin is dominated by the seagrass *Zostera noltii* that accumulates large amounts of silty, organic-matter-rich sediment of up to ~ 1 m thick [33]. Characteristic for intertidal mudflats in general, the morphology throughout the area is typified by gently sloping terrain with shallow overlying relief (< 10 cm; spatial scale: 10–50 m; Figure S2), resulting from sediment trapping by seagrass in interaction with morphodynamics driven by waves, tidal currents, and low-tide dewatering dynamics [11, 34, 35]. Because the die-off was patchy in nature, we first compared the characteristics of degraded patches with

of degradation and our survey in 2012, aboveground seagrass biomass in degraded patches had been reduced by 89% (healthy: 124.3 ± 21.0 g dry weight per m^2 ; degraded: 13.9 ± 6.9 g). Densities of the small (~ 1 cm) dominant lucinid bivalve *Loripes lucinalis* were nine times lower in degraded patches (Figure 4C), while sulfide concentrations in the sediment pore water were over four times higher and showed an increase with depth (Figure 4D). Finally, a comparison of patches sampled both before (2009) and after the collapse (2013) confirmed that lucinids declined dramatically (four to five times) in degrading patches while remaining stable in healthy patches (Figure S3).

DISCUSSION

Our findings of feedback-mediated seagrass decline, combined with low lucinid numbers and high sulfide levels following the 2011 drought, provide evidence that this climatic event initiated the sudden failure of a facultative mutualism that in turn exacerbated the observed collapse. Local climate data combined with NDVI and potential analyses suggest that seagrass degradation was initially triggered by desiccation induced by high evapotranspiration (evaporation plus plant transpiration) during drought. After the onset, however, the decline persisted in the

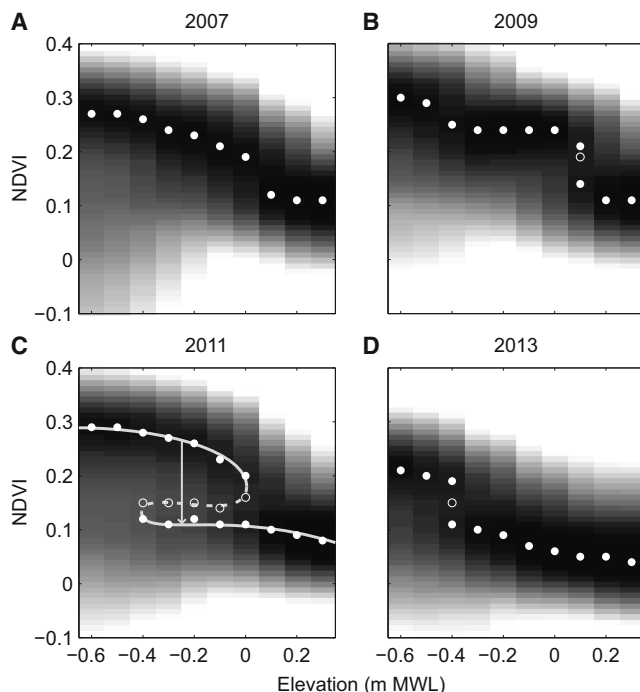


Figure 3. Potential Analyses on NDVI across Elevation from 2007 to 2013

Dark and light shades depict NDVI ranges of high and low occurrence, respectively; closed and open markers depict “attractors” (peaks in occurrence) and “repellers” (lows in occurrence) that are automatically identified by the analysis per 0.1-m elevation interval. In 2007 (A) and 2009 (B), the analysis identified only a single high-NDVI attractor (>0.2) at low elevations and a low-NDVI attractor (~ 0.1) above mean water level (MWL). For 2011 (C), the analysis reveals the existence of two distinct stable attractors at intermediate elevations, with unstable repellers in between. In 2013 (D), only the lower attractor was stable above -0.4 m MWL. Overall, the analyses combined indicate that the 2011 drought triggered a feedback-mediated transition at intermediate elevations from a state of high seagrass cover to a degraded state, as manually illustrated in (C). Solid and dashed gray lines depict stable equilibria and transition thresholds, respectively; the gray arrow indicates the direction of the shift.

years following the drought, and potential analyses suggest that disruption of internal feedback mechanisms played an important role in the observed collapse.

Clearly, although the potential analysis reveals that the observed collapse was mediated by internal feedbacks, it provides no indication of which feedbacks were involved. A likely contributing feedback was sediment accumulation by seagrass that hampered seagrass itself: variations in shoot densities in interaction with morphodynamics probably resulted in the observed local sedimentation differences [11, 34, 35], making higher patches more vulnerable to drainage and drought stress. Our field measurements, however, also show that the mutualistic seagrass-lucinid feedback was broken by the drought, as both seagrass biomass and lucinid densities declined dramatically, and that associated accumulation of toxic sulfide probably contributed to the collapse. This suggests that decreased seagrass condition caused by desiccation stress led to decreased photosynthesis-driven oxygen release from the roots, stimulating sulfide production. As an apparent consequence, sulfide oxidation by the lucinid-bacteria diminished, causing sulfide

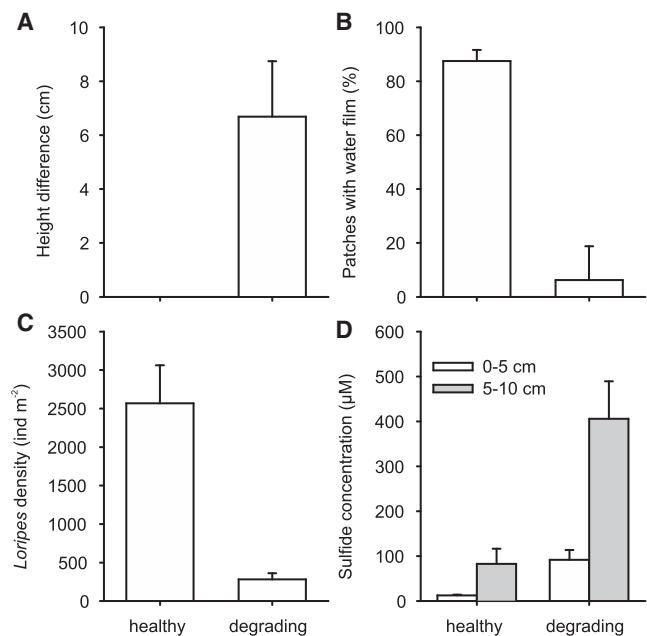


Figure 4. Comparisons of the Environmental Characteristics of Healthy and Adjacent Degrading Seagrass Patches

Degrading patches were elevated compared to healthy controls (A; $F_{1,55} = 60.91$, $p < 0.001$; $n = 32$) and were typically dry, whereas healthy patches were characterized by a thin film of water on the sediment surface (B; $\chi^2 = 7.56$, $p = 0.006$; $n = 32$). Lucinid densities were significantly lower in degrading patches (C; $\chi^2 = 302.69$, $p < 0.001$; $n = 8$), and sulfide concentrations in the pore water were higher (D; $F_{1,14} = 15.99$, $p = 0.001$; $n = 8$). Sulfide levels showed a significant increase with depth ($F_{1,14} = 21.0$, $p < 0.001$; $n = 8$) and an interaction between patch condition and depth ($F_{1,14} = 8.4$, $p = 0.011$; $n = 8$). Error bars depict SEs. See also Figures S1–S3.

accumulation to levels that are known to seriously hamper growth and survival of seagrass in general [20], and in our case to levels twice as high as those previously reported to decrease *Z. noltii* biomass by 30% [3].

Our study, combined with earlier work, highlights the importance of indirect responses of ecosystems to droughts [10]. Desiccation is a well-known stressor in subtropical to tropical intertidal seagrass beds such as Banc d’Arguin where drought and heat waves can cause severe desiccation events, particularly when coinciding with strong winds and neap tides causing prolonged low-tide exposure [15, 24]. Extreme events such as drought, strong winds, and tidal extremes are all predicted to increase in frequency and severity with global warming [36]. Although sea level rise could be expected to mitigate future extreme drought events, expected increases in tidal amplitudes [37] might, depending on local conditions, also further enhance drought stress. Overall, desiccation stress is therefore increasingly considered to become an important threat to intertidal seagrass meadows in warmer regions [15, 16, 24, 38].

Apart from desiccation, there are many other stressors for seagrass beds worldwide that could initiate breakdown of this mutualism, many of which are anthropogenic in origin [13, 39]. For example, eutrophication typically reduces light availability (and thus photosynthesis-driven oxygen release from seagrass roots) due to the higher competitive strength of algae [40], while

sulfide levels may increase as a result of enhanced input of easily degradable algal and other organic matter [20, 40]. Other examples are siltation events reducing light levels [39], salt stress hampering photosynthesis by seagrasses [37], and increased temperature driving enhanced sulfide production [41]. Due to global change, mutualism breakdown and sulfide toxicity may therefore become a more common phenomenon in seagrass meadows, and thus potentially an important factor in the worldwide decline of seagrass ecosystems [13, 39].

Our results point at a hidden risk of mutualism dependency in marine ecosystems that goes beyond the obligate coral symbiosis: environmental change can disrupt facultative mutualistic feedbacks, and this may in turn have important consequences for ecosystem functioning and the provided services (e.g., biodiversity enhancement, carbon and nutrient storage, food and water supply, and flood protection) [13, 14, 42]. Indeed, many marine ecosystems with mutualisms, such as coral reefs, seagrass meadows, kelp forest, salt marshes, and mangroves, have declined dramatically due to global change (e.g., global warming, eutrophication, and overfishing) over recent decades [13, 42]. Clearly, the importance of mutualisms for ecosystem functioning, as well as their role in ecosystem losses, needs a better understanding. As mutualism breakdown is likely to become more common in a future governed by global change [4], we suggest that these mechanisms need to be included in marine conservation and restoration approaches.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.02.023>.

AUTHOR CONTRIBUTIONS

J.d.F., T.v.d.H., L.L.G., A.J.P.S., and L.P.M.L. designed the study. J.d.F., T.v.d.H., L.L.G., M.A.S.C., M.J.A.C., K.J.v.d.R., M.v.d.G., H.O., and J.A.v.G. collected data. J.d.F., T.v.d.H., J.v.B., and W.D. conducted analyses. J.d.F. and T.v.d.H. wrote the first draft of the paper, and all authors contributed substantially to revisions.

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